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Modeling Mojave Desert Tortoise Population Response to Anthropogenic Stressors

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ABSTRACT Mojave Desert tortoise (*Gopherus agassizii*) populations are exposed to a variety of anthropogenic threats, which vary in nature, severity, and frequency. Tortoise management in conservation areas can be compromised when the relative importance of these threats is not well understood. We used HexSim to develop simulation models for desert tortoise populations occupying two distinct study areas in the western-central (Superior Cronese) and the eastern (Gold Butte-Pakoon) Mojave Desert. The threats impacting tortoises vary by study area, and we conducted independent simulations of for each region. Tortoises in both regions were impacted by threats associated with human presence, and by subsidized predators. Additional threats in the Superior Cronese region included disease and habitat degradation on land in-holdings, whereas Gold Butte-Pakoon tortoises were further exposed to wildfire, livestock grazing, feral burros. We used our two study area-specific simulation models to rank the threats' relative importance to desert tortoise population viability. We found that threats more uniformly distributed in time and space tended to have more severe impact on tortoise populations compared to threats that were unevenly distributed or temporally dynamic. Our threat prioritization will inform and improve ongoing management efforts attempting to increase desert tortoise population viability by altering anthropogenic disturbance regimes.

KEYWORDS HexSim, *Gopherus agassizii*, Mojave Desert tortoise, population model, anthropogenic threats.

We used individual-based, spatially explicit population models to rank the relative importance of multiple anthropogenic stressors to Mojave Desert tortoise (*Gopherus agassizii*) populations at two conservation areas on lands largely managed by the Bureau of Land Management (BLM) in the Mojave Desert. The Mojave Desert tortoise (MDT), which inhabits the Mojave and Colorado Deserts in California, Nevada, Utah and Arizona, was listed as a Threatened species in

1990 following major declines in population density throughout the western part of the species'

range (U.S. Fish and Wildlife Service [USFWS] 1994). MDT population declines in the Mojave

Desert since the 1970s have been attributed to the cumulative impacts of numerous distinct

threats, and are frequently characterized as a "death by a thousand cuts." In its final listing

decision (USFWS 1994), the USFWS attributed MDT population decline to two major factors:

1) habitat loss and degradation caused by human activities such as off-highway vehicle use,

urbanization, agriculture, energy development, military training, mining, and livestock grazing;

and 2) mortality of directly attributable to upper respiratory tract disease, increased predation by

common ravens (*Corvus corax*), collection by humans for pets or consumption, and collisions

with vehicles on paved and unpaved roads (USFWS 1990). More recent threats reviews

(Boarman 2002; Tracy et al. 2004; USFWS 2011) describe the cumulative effects of dozens of

distinct stressors, most of them anthropogenic in origin.

Mojave Desert tortoise populations face an assortment of anthropogenic threats that individually

and cumulatively contribute to population decline. Each threat varies in both its detrimental

effects to MDT populations, and its severity and distribution in time and space. Managing

threats at the local level is problematic at best; while information about the effects of some

threats may be available, knowledge of the relative importance of numerous threats is generally

unavailable. Identifying causal relationships between individual threats and population decline is

critical to the effective prioritization of recovery efforts and funding; however, traditional field-

based studies have thus far failed to identify these relationships. Mojave Desert tortoises are

characterized by high survivorship of long-lived adults (Turner et al. 1984), but low female

fecundity rates (Turner et al. 1986; Mueller et al. 1998; Wallis et al. 1999), low survivorship

rates of eggs and juveniles (Bjurlin and Bissonette 2004), and slow growth and delayed maturity

(Turner et al. 1987) These life history attributes are associated with long time lags separating a disturbance from its population-level consequence (citations on extinction debt), making it difficult for comparatively short-term field-based studies to quantify the impacts of specific threats. The use of mechanistic population models can overcome these deficiencies of field-based studies, helping researchers to link anthropogenic threats to population decline (citations – examples of the application of population models to quantify threats).

Recent advances in simulation modeling make it possible to quantify the population-level impacts of single threats in isolation, as well as multiple threats in concert. But population modeling has long been employed in the pursuit of a better understanding of turtle population dynamics. Spatially implicit, stage-based population modeling has been applied to sea turtle (Crouse et al. 1987; Crowder et al. 1994; Heppell 1998; Chaloupka 2002) and diamondback terrapin populations (Mitro 2003) to guide conservation and management practices. Mazaris et al. (2005) used a spatially implicit, individual-based model to inform management practices for loggerhead sea turtle populations, and Mazaris and Matsinos (2006a; 2006b) used this approach to simulate population response to variations in environmental conditions and survivorship among age classes for green sea turtles. Spatially-implicit population models have also been used to identify sensitive age and sex categories within MDT populations that should be targeted for conservation and management measures (Doak et al. 1994; Wisdom et al. 2000; Reed et al. 2009). More recently, spatially explicit models have coupled landscapes to demographic processes and movement behaviors, making it possible to better quantify the population-level impacts of spatially variable environments. Spatially explicit models have also been used to examine relationships between habitat loss and connectivity between gopher tortoise populations

(BenDor et al. 2009), and extirpation probabilities for spotted turtle populations within isolated ponds (Enneson and Litzgus 2009).

The goal of this study is to use a spatially-explicit individual-based population model to overcome the limitations that have characterized earlier threat analyses and spatially implicit modeling efforts. Our approach is unique because it treats anthropogenic disturbance as site-specific and dynamic, and because our simulated stressors can be coupled or decoupled. Previous threat reviews can be found in USFWS recovery plans (USFWS 1994b; USFWS 2011, Appendix A) and reviews by the US Geological Survey (Boarman 2002) and the Desert Tortoise Recovery Plan Assessment Committee (Tracy et al. 2004). These reviews (excepting Boarman's), did not discuss how threats may vary in severity or distribution across the range of the MDT, nor do they prioritize the importance of the threats. These model limitations in turn constrain the utility of species conservation measures developed from their results. Because federal lands supporting MDT populations are managed at the local level, and since threats to tortoise populations vary in occurrence, distribution, and severity across the range of the species, federal land managers need an understanding of population response to threats at a local scale. With knowledge of the types of threats, their distributions within MDT conservation areas, and the manner in which they combine to produce cumulative effects, land managers and wildlife biologists could identify and prioritize management techniques and measures that should be implemented to enhance population recovery at the local level.

STUDY AREAS

We modeled MDT populations within two study areas: the Superior-Cronese and Gold Butte-Pakoon conservation areas (Figure 1). The 629,697 acre Superior-Cronese study area is situated

in the western and central Mojave Desert and within the Western Mojave Recovery Unit, and is largely comprised of BLM-managed federal lands within the USFWS-designated Superior-Cronese Critical Habitat Unit. The Superior-Cronese study area is characterized by substantial (>35% by area) ownership of non-BLM lands distributed among more than 200 small private, state, and federally owned land in-holdings in a checkerboard-like fashion and totaling 224,744 acres. Prominent land uses in the Superior-Cronese study area include off-highway vehicle use, utility development, military activities, mining, and agriculture. Urbanization in the study area's vicinity includes the city of Barstow, California and its outlying communities. Other environmental stressors that affect Mojave Desert tortoise populations in this study area include predation by human-subsidized predators (Boarman 1993; Boarman et al. 1995; Esque et al. 2010) and mycoplasmosis respiratory disease (Berry et al. 2006), which are both more prevalent within tortoise populations near urbanized areas.

The 611,358 acre Gold Butte-Pakoon study area is situated within the eastern Mojave Desert and located within the USFWS-designated Northeastern Mojave Recovery Unit and within the USFWS-designated Gold Butte-Pakoon Critical Habitat Unit, and is comprised predominantly of federal lands within several BLM-designated Areas of Critical Environmental Concern, a BLM-designated Wildlife Habitat Area, and several executively-designated Wilderness Areas in southern Nevada and northwestern Arizona. A portion of the study area in Arizona is jointly managed by the National Park Service, where the executively-designated Grand Canyon-Parashant National Monument and Lake Mead National Recreation Area encompass it. Prominent and ongoing land uses in the Gold Butte-Pakoon management area include livestock grazing and off-highway vehicle use. Urbanization in the study area's vicinity includes the city of Mesquite, Nevada and its outlying communities. Portions of the study area have been ravaged

by wildfire in recent decades, including low-elevation areas supporting Mojave Desert tortoise

habitat.

METHODS

We developed two models for each study area: a tortoise predictive occurrence model and a

tortoise population model. The predictive occurrence models (described below) estimate the

potential for occupancy by tortoises from habitat structure and tortoise census data. We

imported the occurrence models into a mechanistic population model (see below) that simulated

individual movement, survival, and reproductive decisions. We parameterized vital rates and

movement behaviors within the population model using existing information about Mojave

Desert tortoise biology and life history traits. We developed a disturbance-free "baseline"

population model as a reference to assess the degree to which threats affected population

stability. We simulated the threats separately so that each could be individually ranked by its

importance as a cause of MDT decline.

Our MDT predictive occurrence models were constructed using stepwise logistic regression to

compare known presence and absence locations to the availability of mapped habitat elements.

The regression models generate an estimated probability of MDT occurrence within each 30 m^2

cell of the gridded study areas. The USGS previously developed a similar predictive occurrence

model for desert tortoises using this technique (Nussear et al. 2009), but their model was

developed across the range of both the Mojave and Sonoran Desert tortoises, at a courser spatial

resolution (1 km).

We developed the predictive occurrence models using a raster data structure, which divided each study area into a grid of 30 m cellsindicating MDT presence or absence.   The Superior-Cronese and Gold Butte-Pakoon study areas each contained >4.2 M grid cells.

We determined tortoise presence within each cell from census surveys of study plots, independent radio telemetric observations, opportunistic field observations, and previously collected occurrence data. Since each grid cell was scored as either a presence or an absence, the tortoise presence metric was independent of the number of observations within the cell.   To reduce spatial autocorrelation, we included any adjoining presence cells together in the same dataset. We selected random absence points within study area cells stratified by 'non-tortoise habitat.' We designated zones of tortoise absence within each study area based upon the spatial arrangement of habitats that cannot support their occurrence, such as high-elevation montane habitats and wetlands. These areas served as stratified zones for random sampling of absence points. Absence cells generated with this technique were supplemented with confirmed absence data determined during census surveys of study plots within each study area. We selected absence cells to provide a ratio (absence cells: presence cells) of no more than 2:1 to avoid saturating the model with absence data. We randomly assigned the presence/absence data to one of two datasets. We developed a preliminary predictive occurrence model with the first dataset and tested it with the second dataset.

We developed the predictive occurrence models with datasets included precipitation data, topographic data, biotic data, and geomorphologic data (Table 1). Once we created the rasters for each of the mapped habitat elements, we tabulated their presence (1) or absence (0) within each cell in a matrix for statistical analysis. We used the JMP 10 statistical package to apply the stepwise logistic regression and develop the probability equations for tortoise presence and

absence against these variables. The equations were applied to the grid dataset (in GIS) to

generate tortoise occurrence probability (ranging from 0 to 1) within each cell. We converted

this probability raster into a shape file depicting ten categories of probability (0-0.10, 0.10-0.20,

etc.). We then used the second set of tortoise presence/absence data to test the accuracy of the

model's predictions. Following Kvamme (1988:329), we employed the gain statistic, which

allowed us to gauge the efficiency of the model by comparing the area where tortoises are

predicted to occur with the actual number of tortoises in the predicted occurrence areas.

We produced raster images of the predictive occurrence models and imported them into the

HexSim population model as the primary base layers (spatial environment) for each model.

HexSim converts raster data into a lattice of hexagonal cells, with each cell assigned a numerical

value derived from the raster image (using mean, mode, or other operators). We assigned the

hexagons a width of 150 m (between parallel sides), which corresponded to an area of 1.95 ha.

We considered this resolution appropriate for modeling the space use behaviors of individual

tortoises. The raster image of the original predictive habitat model is composed of 30 m cells

(squares), each embedded with continuous data distributed from 0.0 to 1.0 corresponding to a

probability for tortoise occurrence. Each hexagon's score was set equal to the model of the

occupancy map pixels that it circumscribed, and the resulting hexagon map thus retained the

binary character of the original occupancy map.. We then converted the scores within the

HexMap to a categorical, integer-based scale that included the following categories: 1-9; 10-19;

20-29; 30-39; 40-49; 50-59; 60-69; 70-79; 80-89; and 90-100. Values less than 20 were

excluded from the use area for tortoises by scoring them as '1' and defining them as

uninhabitable. The area outside of the study area was scored '0' to exclude any tortoise activity

from this area.

The scores within the hexagons pertained to the amount of available resources, and therefore, the greater probability of inhabitancy by a tortoise. We assumed that the primary resource that tortoises would seek out within their resource acquisition areas were cover sites, i.e., burrows and caves. Accordingly, we parameterized the model to allow a greater density of tortoises in areas that contained higher scores within hexagons.

The resource scores within each hexagon describe the amount of resources available to tortoises during each time step, which we defined as one year. We parameterized tortoise behavior so it would be affected by the resource quality of the hexagons they occupied. This allowed us to place limits on tortoise population density based on rules set for reproduction. We know from literature that a density of 50 tortoises per km^2 is achievable (Berry 1984), so we set that density as our limit in the baseline model. Since the model is female only, we set the maximum density at 25 tortoises per km^2, or one tortoise per two hexagons. To achieve this maximum density, we parameterized tortoises to acquire a target resource value of 200. In other words, we assume hexagons with a score of 100 are capable of supporting the maximum population density of 50 tortoises per km^2.

We allowed females to acquire resources from a maximum of five hexagons per time step by setting both the 'range' and 'explored area' to five ('range' in HexSim corresponds to an ecological territory and 'explored area' corresponds to an ecological home range). HexSim allows explored areas (home ranges) to overlap, but ranges (territories) do not. In our model, each tortoise's range is derived from the explored area so that multiple tortoises are able to search for resources in the same location but ultimately only one tortoise will occupy a given area (i.e. have the hexagon included in their range). Since the highest resource value per hexagon is 100, one female can acquire her target resources within a minimum of two hexagons

during each time step. In lower quality habitat (hexagon scores less than 100), females would

need to occupy more hexagons to achieve a score of 200. Because there is a maximum limit of

five hexagons in which the score of 200 can be achieved, the resource target will not be reached

for any home range in which the maximum hexagon score in their explored area is below 40 (i.e.

a deficient home range).

If a female is unable to achieve her target resource within five hexagons during a time step she

becomes a 'floater' or a non-reproducing individual. Furthermore, we imposed a decreased

probability of survival (-0.01) for floaters, i.e. tortoises with deficient home ranges. In our model

this is the primary mechanism we used for imposing density-dependent feedback on population

growth. All females that met their resource targets per time step were subject to reproduction

rates (described below). Only adult female tortoises were required to acquire target resources;

this allowed immature tortoises to occur within hexagons without limits on density, and without

competing with adults.

Survival and reproductive rates varied by age (or should it be stage) class (you need to describe

the stage classes before getting to this sentence). We based the survivorship of neonates on field

data presented by Bjurlin and Bissonette (2004). Data for other juvenile Mojave Desert tortoise

age classes are generally lacking, though studies of chelonian species indicate relatively high

mortality until maturity (Wilbur and Morin 1988; Brooks et al. 1991; Congdon et al. 1993;

1994). We parameterized survivorship rates in a manner that gave increasing survivorship to

increasingly older age classes, but also produced a stable population (Table 2). In order to have

modeled tortoises die of 'old age,' we reduced the survivorship of senescent individuals (those

80+ years old). This allowed tortoises to – in the absence of stochastic events – attain ages of

between 80 and 100 years old (although tortoises could, though very rarely, attain ages

exceeding 100 years).

We additionally depressed survivorship rates for certain behavioral categories. As previously

mentioned, we depressed the survival rates for 'floater' tortoises that occupied deficient home

ranges. Finally, we defined a unique survivorship rate for tortoises that could not disperse from

very poor habitat, which we defined as areas where resource scores over a tortoise's range

averaged less than 20 per hexagon. Tortoises that could not disperse from these areas within one

time step were penalized with a lowered probability of survival (by -0.3).

We assigned reproductive rates to the mature tortoise age classes in a manner that approximated

reproductive rates observed by various researchers across the range of the Mojave Desert tortoise

(Table 3). Using these data as a guide to parameterizing the reproductive rates of the modeled

tortoises, we allowed tortoises to lay up to eight eggs per season (Table 4). Since the HexSim

model is a female-only model, the clutch sizes of the modeled tortoises were approximately one-

half of what we expected naturally-occurring wild tortoises to produce. Thus, while previous

researchers have determined that female tortoises produce (on average) between 4.87 and 8.38

eggs per season (Table 3), our modeled tortoises produced (on average) between 2.5 and 4.83

eggs per season (Table 4). To account for a proportion of females within populations that forego

reproduction, we assigned a reproductive rate of 0.0 for a proportion of the modeled females.

We assumed that younger adult females, because of their allocation of a relatively higher

proportion of their annual energy budgets to growth, would forego reproduction more frequently

than older females. Floaters were always assigned a reproductive rate of 0.0.

HexSim allows for dispersal and exploration (construction of home ranges) events, which we used to parameterize movement behaviors for modeled tortoises within home ranges, as well as for age-specific dispersal rates and distances. These parameters were defined at the beginning of each time step, when the modeled tortoises were probabilistically assigned to one of three movement classes: 1) foragers, 2) natal area dispersers, and 3) adult dispersers. We defined 'foragers' as those tortoises that move within home ranges; 'natal area dispersers' as subadults that dispersed from natal areas; and 'adult dispersers' as adult tortoises that made long-distance dispersal movements to new areas to establish new home ranges. For movement classes, we parameterized the maximum number of explorations, dispersal path lengths, directional probabilities, the influence of attraction and repulsion to spatial data, and stopping criteria.

Adult tortoises assigned as 'foragers' at the beginning of a time step were allowed a maximum of four attempts to construct a home range (explored areas) and acquire their resource score of 200 from a maximum of five hexagons per explored area. Home ranges tended to occur within higher quality habitat but the territory acquisition process was imperfect, and thus allowed for the inclusion of some lower quality habitat. We set maximum dispersal paths lengths to 150 m (2 hexagons) for adult foragers. With four exploration opportunities allowed per movement event, each tortoise was allowed to travel up to 1200 m (8 hexagons) in search of a sufficient home range during a time step. Older tortoises were allowed to search for territories first, which preferentially imposed density dependent effects onto the younger age classes. Dispersal paths exhibited limited spatial autocorrelation. We set the home ranges of immature tortoises to one hexagon. Immature tortoises were assigned nominal resource needs so they would not compete with adults.

We constructed a movement class, 'natal area dispersal,' which allowed immature tortoises to disperse from their natal areas. We created a probabilistic function that set a 0.13 probability that each subadult tortoise would be assigned to this movement category per time step. Since subadults were those tortoises between 10 and 16 years (time steps), on average 90% of them dispersed from natal areas using this function. We parameterized the distances moved during dispersal to a range scaling from 300 m (2 hexagons) to 2400 m (16 hexagons). We set the autocorrelation of direction of the dispersal path to 50%. Once dispersed, a subadult was assigned as a forager and assumed the subadult forager movement pattern. The remaining 10% of subadults that did not disperse were converted into subadult foragers within their natal areas. We set the subadult forager movement pattern to maximum path lengths of 300 m per movement, with the directional autocorrelation set to 25%. When a subadult matured (at time step 17), it took on the adult forager movement pattern.

We created a second movement event for adults that allowed them to make long-distance dispersals. We gave every adult a 0.5% chance that it would disperse from its explored area per time step. We parameterized the distances moved during dispersal to a range scaling from 2,250 m (15 hexagons) to 6,000 m (40 hexagons). We set the autocorrelation of direction of the dispersal path to 75%, which allowed for relatively straight movements. Once dispersed, the tortoise returned to the forager movement pattern and was not eligible for another dispersal event.

We scored hexagons with attraction and repulsion parameters to guide tortoise movements away from some landscapes, such as uninhabitable areas where tortoises would not find the habitat elements necessary for resource extraction or survival. We defined these uninhabitable areas as those with hexagons scored less than 20. The adult dispersal movement event allowed tortoises

to traverse lower quality habitat in pursuit of a new home range but without being penalized by the surrounding habitat quality. However, since it was possible for dispersing tortoises to become "stuck" in these uninhabitable zones, we created a dispersal event called 'evacuate uninhabitable areas.' Distances moved during the evacuation dispersal event included a range scaling from 300 m (2 hexagons) to 6,000 m (40 hexagons). We set the autocorrelation of direction of the dispersal path to 80%. We also programmed values defining a 'stopping criteria' for this dispersal event. This function stopped movement when the mean resource score within the traversed hexagons was greater than 40 as experienced over two path lengths. For those tortoises still occupying uninhabitable zones after the evacuation event, we parameterized a penalty of a lowered survivorship rate by -0.3.

We constructed barriers in areas of high slope and high elevation, which essentially prevented tortoises from passage. We used a 30-m digital elevation model to determine areas of elevation greater than 1,220 m (following Bury et al. 1994) and slopes greater than 40 degrees, where we constructed barriers. Thus, barriers were constructed primarily in mountainous areas with precipitous slopes.

In order to validate parameters, identify unrealistic patterns or software-specific errors in events, and develop a final baseline model that produced a stable population, we constructed a series of baseline test models through an iterative process. The test models also allowed us to identify and correct biologically unrealistic behaviors and events, and to incorporate additional events or traits to better simulate reality. We incorporated a series of census events in the test models, which allowed us to validate proper functioning of events. The test models were particularly valuable for parameterizing survivorship rates among age classes, as these rates are generally unknown for wild populations.

Once we developed a population that filled the HexSim environment and achieved and

maintained a stable state over a period of at least 5,000 time steps (years), we collected census

data to determine population size and age class structure. The population sizes at the stable state

were approximately 16,350 individuals for the Superior-Cronese study area and 7,100 for the

Gold Butte-Pakoon study area, which were achieved whether we started the simulations with a

lower or higher population size. At stable state, the proportion of individuals among age classes

was applied to the starting conditions for all subsequent models. Individuals were randomly

assigned specific ages within each age group at start-up, and distributed randomly in space

within hexagons scored 80 or above, i.e. high quality habitat.

We modeled several of the more important site-specific threats to Mojave Desert tortoise

populations within each study area. For the Superior-Cronese study area, we modeled habitat

degradation on land in-holdings, disease, subsidized predators, and human presence. For the

Gold Butte-Pakoon study area, we modeled livestock grazing, wildfire, subsidized predators, and

human presence. For each of the threats models, we introduced mortality and/or habitat

degradation into each baseline population model. We simulated habitat degradation by

subtracting hexagon scores from the baseline habitat HexMap, and increased mortality by

lowering the survivorship of tortoises. We constructed multiple models for each threat that

included varied scales of habitat degradation and mortality, from low effect to severe effect.

A significant portion (224,744 acres) of the Superior-Cronese study area includes privately-

owned land in-holdings. These areas are outside of the management control of the BLM, and

could potentially be developed or converted to a land use that is inconsistent with inhabitancy by

tortoises. We simulated the effects of habitat degradation on these land in-holdings by degrading

tortoise habitat within them. We constructed six models with increasing amounts of degradation

(10 points for each scenario) until habitat values reached the lowest level of habitat quality

capable of sustaining a population (i.e., the highest score within hexagons was 40). We

maintained the same mortality rates that were set the baseline model for this series of models.

We simulated the effects of cyclical disease epidemics in the Superior-Cronese study area by

causing an increase in mortality during modeled outbreaks. We modeled mycoplasmosis, a

disease known to cause upper respiratory tract disease (URTD) in Mojave Desert tortoises

(Brown et al. 1994; Brown et al. 2004), and likely spread through tortoise-to-tortoise contact

facilitated by social interactions (Wendland et al. 2010). We cycled outbreaks to occur over a

five-year period every thirty years. Following Berry et al. (2006), we assumed that incidences of

mycoplasmosis would be most prevalent near the urban-wildlands interface. We modeled 1,000

m zones of increasing survivorship with increased distance from human developments and roads.

We modeled the effects of varying levels of severity of the modeled epidemics by reducing the

mortality rates of adult tortoises in these zones by between l_x - 0.01 and l_x - 0.06. Following

Wendland et al. (2010), we restricted the disease incidence and increased mortality rates over the

baseline model to adult tortoises only.

We simulated the effects of grazing livestock and feral burros in the Gold Butte-Pakoon study

area by degrading tortoise habitat and causing a slight increase in mortality. Based on

differences in management of grazing livestock between the Nevada and Arizona sides of the

study area, as well as field observations of grazing livestock and feral burros and their effects on

habitat there, we ranked the effects of grazing cattle and feral burros for three portions of the

Gold Butte-Pakoon study area: 1) Pakoon Basin in Arizona (high impact); 2) Virgin Slope in

Arizona (medium impact); and 3) Nevada portion of study area (low impact).

We constructed six models that differentially degraded the habitat in these three areas by subtracting 5, 7.5, and 10 points from each hexagon score for the Nevada portion, Virgin Slope, and Pakoon Basin, respectively. We increased the amount of degradation until the habitat within the Pakoon Basin reached the lowest level of habitat quality capable of sustaining a population (i.e., the highest score within hexagons was 40). We increased mortality slightly on the Virgin Slope (l_x - 0.01) and the Pakoon Basin (l_x - 0.03).

We simulated the effects of periodic wildfire in the Gold Butte-Pakoon study area by degrading tortoise habitat and causing an increase in mortality. We modeled the effect of fires in areas and at frequencies that previously burned in the study area between 1990 and 2010. We modeled the effects of habitat degradation in three-year increments according to the fire frequency, i.e., areas that burned once were subjected to lowered habitat values for three years, those that burned twice for six years, and those that burned three times for nine years. We applied these habitat values within burned areas over a 20 year cycle. After nine years, all habitat effects of fire were removed until the cycle started again. We modeled varying effects of wildfire on habitat degradation until the highest score within hexagons was 30, the point at which all tortoises inhabiting the area would be converted to floaters. This produced a total of seven models. We also modeled the effects on survivorship on a 20-year cycle, but the values were only applied during the time step that the fire occurred (up to three times per 20 year cycle). We modeled three scenarios of different survivorship rates (l_x - 0.1, l_x - 0.15, and l_x - 0.2) which, when combined with the habitat degradation scenarios, produced a total of 21 wildfire models.

We simulated the effects of subsidized predators in both study areas by decreasing survivorship in affected areas, which we assumed would occur in the vicinity of anthropogenic food and water sources. We modeled affected areas by placing buffers around features that provide subsidies for

ravens and coyotes (as well as other canids). These included urbanized areas, landfills, and anthropogenic sources of water (including cattle troughs). We established 4.46 km buffers around these features, based upon the Boarman et al. (1995) study of telemetered ravens and their use of human subsidies in the western Mojave Desert. Little is known about the movements and ranging behaviors of coyotes in the vicinity of urban areas in the Mojave Desert, but an example from of Tucson, Arizona in the Sonora Desert indicates that telemetered coyotes generally ranged within 5 km of urban areas (Grinder and Krausman 2001). We modeled the effect of increased raven predation on tortoises less than 110 mm in length in affected areas using three scenarios of varying severity. Tortoises less than 110 mm carapace length were subjected to increased mortality rates of l_x - 0.1, l_x - 0.15, and l_x - 0.2 for each scenario. We modeled the effect of increased coyote and feral dog predation on all age classes in affected areas, also using three scenarios of varying severity, with mortality rates reduced by l_x - 0.1, l_x - 0.15, and l_x - 0.2 for each scenario.

We simulated the effects of human presence in both study areas by degrading tortoise habitat and decreasing survivorship in affected areas. We modeled the effects of human presence adjacent to urbanized areas, roads, trails, recreation areas, mines, utilities, military training areas, and other human developments. We placed buffers of 1500 m around urban areas and homestead developments, 50 m around trails used by off-highway vehicle recreationists, and varying distances from roads (1,400 m, 2,250 m, 2,650 m, and 4,250 m) according to von Seckendorff Hoff and Marlow (2002), who analyzed the tortoise 'mortality sink' around highways and roads in the western and central portions of the Mojave Desert. We constructed a total of 12 models that tested six levels of habitat degradation and two levels of increased mortality. We modeled varying effects of human presence on habitat degradation until the highest score within hexagons

was 30, the point at which all tortoises inhabiting the area would be converted to floaters. These six scenarios of habitat degradation combined with three mortality scenarios (1_x - 0.0, l_x - 0.01, and l_x - 0.05) to produce 18 human presence models.

We performed 10 replicates for each threats scenario, for a total of 60 simulations. Each simulation was run for 2500 time steps. We developed a total of 90 replicates for the human presence scenarios, and 210 replicates for the wildfire scenarios. Threats were introduced after simulation time step 1000, which gave the models time to reach steady-state in the absence of disturbance.

We analyzed the effects of the threats by comparing the absolute difference between the baseline (pre-disturbance) model and each of the threats models. We compared maximum population size within the first 1,000 time steps to the minimum population size in the 1,500 time steps of each replicate after the threats scenario was introduced. We also compared the median of the first group of 1,000 time steps to the median of the second group of 1,500 time steps. We analyzed the maximum difference and median difference scores using analysis of variance (ANOVA). We developed a Bonferroni-corrected multiple comparison following the ANOVA. We also developed descriptive statistics (means and ranks) for each threat scenario.

RESULTS

The purpose of developing separate threat models for each of the study areas was to determine their relative importance in causing Mojave Desert tortoise population decline in the modeled environments. Each of the modeled threats affected the baseline models for each study area differently, though all of the threats caused population decline. For the Superior-Cronese study area, the most severe threat model, or the model that caused the most precipitous and significant

decline of the baseline population model, was human presence (Figure 2a). The second most

important modeled threat in causing decline of the baseline population was subsidized predators

(Figure 2b), followed by the disease (Figure 2c), and habitat degradation on land in-holdings

(Figure 2d) models. For the Gold Butte-Pakoon study area, the most severe threat model was

grazing livestock and feral burros (Figure 3a), followed by the human presence (Figure 3b),

subsidized predators (Figure 3c), and wildfire (Figure 3d) models. Each of the threats models

produced declines that were statistically different from the baseline models for each study area.

The descriptive statistics, which included the means of the maximum and median differences

between the baseline model (first 1,000 time steps) and the threats scenarios (time steps 1,001

through 2,500) are presented in Table 5.

The ANOVA showed that the differences between the threats scenarios for the Superior-Cronese

study area, both by maximum difference (F[3, 416, 419]=1,342.9, p<0.001) and median

difference (F[3, 416, 419]=1,798.2, p<0.001), were significant (Table 6). Similarly, the

differences between the threats scenarios in the Gold Butte-Pakoon study area were significant,

both by maximum difference (F[3, 416, 419]=1,342.9, p<0.001) and median difference (F[3,

416, 419]=1,798.2, p<0.001) (Table 6).

In addition, each of the threats models produced population declines that were largely

significantly different from each other at each study area, which allowed us to confidently rank

their importance in producing population decline. The Bonferroni multiple comparison

correction indicated significant differences between each of the threats models at each study area

when comparing median differences (Table 7). When comparing maximum differences of

threats models for each study area, differences between threats models in the Gold Butte-Pakoon

study area were significant; however, in the Superior-Cronese study area, the human presence

and subsidized predator models were not significantly different from each other, nor were the

disease and habitat degradation on land in-holdings models significantly different from each

other (Table 7).

DISCUSSION

Population modeling is a widely used technique among wildlife biologists, ecologists, and

conservation biologists, as their forecasting capabilities allow for the development of more

informed decisions pertaining to the management of rare species (Bakker et al. 2009). While

spatially implicit population models have played a larger role in guiding these decisions for the

past 25 years, spatially explicit models have recently shown to be powerful tools, particularly for

simulating population dynamics over changing landscapes. In a comparison of spatially explicit

vs. spatially implicit population models, Jager et al. (2005) determined that changes in landscape

characteristics, such as habitat degradation, produced a greater range of population responses in

spatially explicit models than could be detected with spatially implicit models. Spatially explicit

models are additionally capable of modeling population outcomes across landscapes of small to

large scales, and may be used to guide land management and species conservation

recommendations for populations and communities occupying landscapes of all sizes.

Wildlife biologists and ecologists have had great success using HexSim to model population

dynamics over dynamic, patchy, and/or fragmented landscapes as a means to develop

conservation and management recommendations for species and communities. For example,

Heinrichs et al. (2010) used HexSim in combination with a habitat-occurrence model to evaluate

how habitat quality affects population dynamics of the Ord's kangaroo rat in Alberta, Canada.

As well, Marcot et al. (2013) used HexSim to evaluate the effect of habitat patch size and

spacing on northern spotted owl population dynamics. HexSim has been especially useful for

evaluating the dispersal of individuals over dynamic and the effect of species' dispersal abilities

in contributing toward population persistence. For example, Richards et al. (2002) used PATCH

to simulate the dispersal of hypothetical wildlife species within a modeled western Oregon

landscape. Similarly, Carroll et al. (2004) used PATCH to evaluate trends of carnivore dispersal

and population persistence under several scenarios of habitat connectivity over a network of

conservation lands (parks) within the Rocky Mountain region. More recently, Stronen et al.

(2012) simulated population dynamics and dispersal success of wolves across landscapes that

inhibited dispersal through fragmentation and other anthropogenic land uses, features, and

activities that cause "landscape resistance" to dispersal. HexSim has been used to evaluate the

effect of conservation techniques on species recovery, such as wolf reintroduction programs at

various locations in Yellowstone National Park (Carroll et al. 2003a) and across the western

United States (Carroll et al. 2006) as a means to develop reintroduction strategies and programs,

and to test whether habitat quality indices are useful indicators of population viability for hawks

inhabiting habitat patches in eastern United States (Lawler and Schumaker 2004). Importantly

for the current discussion, researchers have previously evaluated the effects of threats to

populations using HexSim in order to develop management and conservation priorities.

Rustigan et al. (2003) used PATCH to model the effects of alternative energy developments

(wind turbines and associated facilities) and other land use futures on amphibian populations

within two watersheds in central Iowa. Carroll et al. (2003b) used PATCH to model carnivore

population response to alternative landscapes in the Rocky Mountain region to develop a

conservation plan that included recommendations for reserve areas. Similarly, Schumaker et al.

(2004) used PATCH to model various species' responses to development within the Willamette

Basin of Oregon. McRae et al. (2008) used PATCH in combination with a climate model to

evaluate songbird species population responses to anthropogenic land use threats in western

Oregon. And Wisley (2011) used HexSim to evaluate black-capped vireo population responses

to anthropogenic land-use, wildfire, and brown-headed cowbird management on the endangered

Black-capped Vireo in central Texas.

Previous population modeling efforts conducted to assess Mojave Desert tortoise population

response to stressors or management techniques were all spatially implicit. Two of these studies

evaluated the effects of implementing management techniques. Wisdom et al. (2000) conducted

a spatially implicit life-stage simulation analysis to evaluate Mojave Desert tortoise vital rates

were most sensitive to manipulation as a way to determine which life-stage would respond best

to conservation techniques and programs. Their results indicated that conservation techniques

directed at any of the tortoise life-stages would result in population growth, but they concluded

that conservation efforts should be directed at adult tortoises. Reed et al. (2009) performed a

spatially implicit vital rate individual-based sensitivity analysis to evaluate the effectiveness of a

variety of Mojave Desert tortoise population conservation techniques over 5, 25, and 50-year

periods. They determined that efforts directed at increasing tortoise nutrition or forage required

sustained management; that increasing the survivorship of adult females would result in highest

population growth; that release of adults into a population (translocation) was more effective

than releasing juveniles (head-starting) in achieving population growth; and that head-starting a

large number of hatchlings at one time was just as effective as annual releases of fewer

individuals. Just one prior modeling effort evaluated the effects of anthropogenic threats to

Mojave Desert tortoise populations. Doak et al. (1994) conducted a spatially implicit sensitivity

analysis of vital rates among eight age/size classes of tortoises as a means to determine which

class was most important for maintaining population growth and most responsive to conservation efforts. They recommended that land use planning and scientific research efforts should focus on eliminating or mitigating the major sources of adult tortoise mortality, such as shooting, OHV use, and URTD.

Despite its wide use, population modeling has its limitations, primarily due to the difficulty of including uncertainties and stochasticity that exist in complicated natural systems, but are difficult or impossible to parameterize in models. As such, though population modeling efforts attempt to simulate reality, their results do not indicate how populations have responded or will respond to environmental perturbations. Population models are a useful way to develop hypotheses concerning natural ecological processes, and the predictive power of population models may be strengthened by testing hypotheses with field data. The current population modeling effort compared various scenarios of population response to anthropogenic threats. The modeled threats were applied individually to a stable modeled population individually in order to determine their relative effects in causing population decline. Thus, while the modeled population response would be a poor predictor of actual response in real populations, this technique was useful for ranking the importance of the threats in order to derive preliminary management prescriptions. Subsequent field data collection may be used to test these conclusions and strengthen the models, which may provide more informed management decisions.

Our modeling effort indicated that threats with wider spatial distributions and more constant occurrence in time were much more important in limiting population growth than those that were patchily-distributed over a limited area and/or cyclical in temporal occurrence. For example, population modeling in the Gold Butte-Pakoon study area indicated that livestock grazing, which

was modeled as a widespread, constant threat with effects that included both habitat degradation and a small increase in tortoise mortality, was more important in causing tortoise population decline than human presence and subsidized predators, which caused constant (and higher) mortality rates, but were patchy in distribution. Wildfire caused both higher mortality and habitat degradation, but was less important because of its cyclical nature and occurrence within small patches.

The picture in the Superior-Cronese study area was more complex. Though all threats there were modeled as patchily-distributed, human presence was most important because it contributed to both habitat degradation and higher mortality rates constantly in time, whereas the second-ranked threat, subsidized predators (a constant threat), caused higher mortality, but not habitat degradation. The disease model also caused higher mortality and no habitat degradation, but because it was modeled as cyclical in nature, was less important. Finally, the threat of habitat degradation on land in-holdings was patchy and constant, but did not contribute to tortoise mortality. Thus, for threats with patchy spatial distributions, those with a constant temporal occurrence that caused both higher mortality rates and habitat degradation (human presence) were more important than constant threats that caused mortality alone (subsidized predators), which were in turn more important than cyclical threats that caused mortality alone (disease) and those that caused habitat degradation alone (habitat degradation on land in-holdings).

Management Implications

The results of our population modeling effort allowed us to rank the importance of site-specific threats within each study area, and set the stage for a re-evaluation of management priorities. Prior researchers used spatially implicit models to develop conservation strategies for Mojave

Desert tortoise populations, and recommended efforts that increase survivorship or decrease mortality of tortoises, particularly for adult females (Doak et al. 1994; Wisdom et al. 2000; Reed et al. 2009). Our use of a spatially-explicit model allowed us to observe simulations of tortoise population dynamics in response to anthropogenic threats over a landscape, and develop new recommendations for Mojave Desert tortoise management and conservation. Our results suggest that threats causing habitat degradation and very slight increases in tortoise mortality over a broad area, such as livestock grazing and illegal off-road vehicle use, are likely more important contributors to tortoise population decline than patchily-distributed threats that cause high mortality rates, such as the presence of subsidized predator populations or road mortality, or cyclical events that cause high mortality (disease, wildfire). Patchily-distributed threats that cause habitat degradation alone are probably the least important type of threat. Based on these results, we recommend that land and wildlife managers focus their priorities for tortoise conservation on efforts that reduce threats that are wide in distribution, constant in occurrence, and cause both an increase in mortality and habitat degradation. Thus, threats such as livestock grazing, off-road vehicle use, and military training, which generally occur over large areas and cause both tortoise mortality and habitat degradation, should be prioritized. Predation of tortoises by human-subsidized predators, which is generally constantly present in the environment, should also be considered an important threat, but because of the patchy nature of this threat and its lack of contribution to habitat degradation, is secondary in importance. A tertiary level of threats includes those that are cyclical in nature and cause tortoise mortality, including disease outbreaks and wildfire. Finally, threats that are patchily-distributed and cause habitat degradation alone should be considered last in priority.

Acknowledgments

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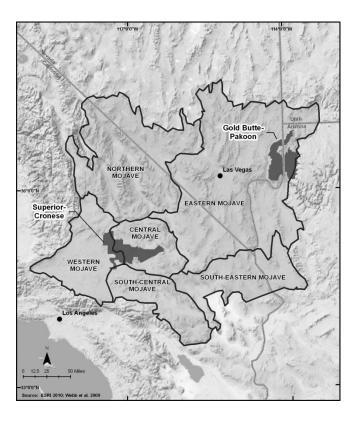
Associate Editor:

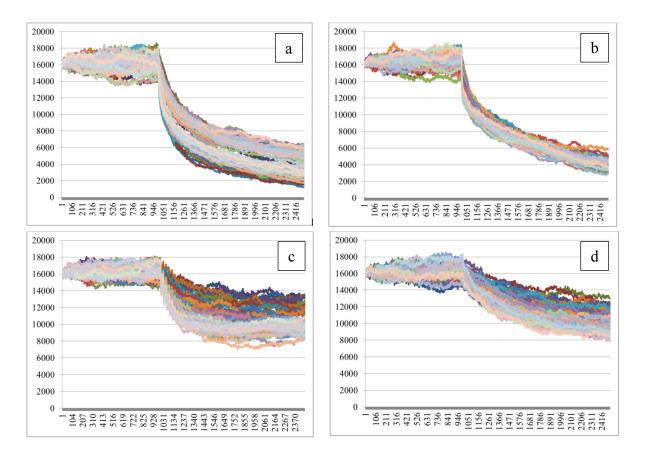Figure 1. Location of the Superior-Cronese and Gold Butte-Pakoon study areas.

Figure 2. Display of replicates of the stable, baseline desert tortoise population model for the Superior-Cronese study area responding to threats models for (a) human presence, (b) subsidized predators, (c) disease, and (d) habitat degradation on land in-holdings introduced at time step 1,001.
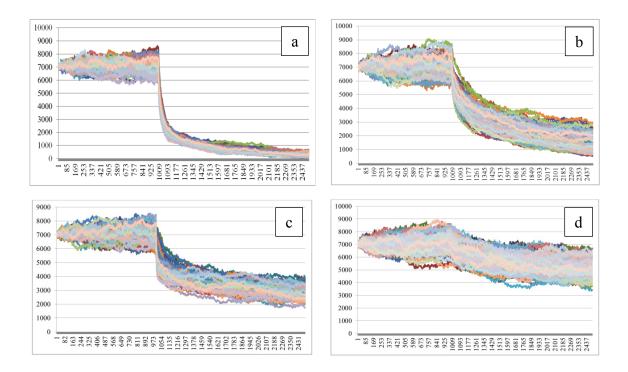
Figure 3. Display of replicates of the stable, baseline desert tortoise population model for the

Gold Butte-Pakoon study area responding to threats models for (a) livestock grazing and feral

burros, (b) human presence, (c) subsidized predators, and (d) wildfire introduced at time step

1,001.

Table 1. Habitat elements chosen for modeling desert tortoise predictive occurrence.

Habitat elements	Data Type
Average annual rainfall	Continuous Variable (avg. prec. accum.)
Winter precipitation (November through February)	Continuous Variable (avg. prec. accum.)
Summer precipitation (June through September)	Continuous Variable (avg. prec. accum.)
Vegetation communities	Discrete Variable (14 categories)
Elevation	Continuous Variable (in m)
Aspect	Discrete Variable (8 categories)
Slope	Continuous Variable (in m)
Surface roughness	Continuous Variable (in m)
Soil parent material	Discrete (3 categories)
Soil pedogenic setting	Discrete (4 categories)
Soil caliche potential	Discrete (3 categories)
Geology	Discrete (17 categories)

Table 2. Survival rates for tortoises in the baseline population model.

Age Class	Survivorship Rate
Neonates (0-1 year)	0.4
One-year olds (1-2 years)	0.5
Juveniles (2-6 years)	0.68
Subadults (7-16 years)	0.88
Young adults (16-29 years) [Floater]	0.96
Young adults (16-29 years)	0.97
Middle-aged adults (30-59 years) [Floater]	0.98
Middle-aged adults (30-59 years)	0.99
Old adults (60-79 years) [Floater]	0.98
Old adults (60-79 years)	0.99
Senescent adult (80+ years) [Floater]	0.73
Senescent adult (80+ years)	0.74

Table 3. Reproduction rates for female desert tortoises at several Mojave Desert study sites.

Population	Study vicinity	Proportion of sample that did not reproduce	Mean clutch frequency	Size of first clutch	Size of second clutch	Size of third clutch	Mean number of eggs per female per year ± SD
Goffs – 1983 (Turner et al. 1986)	Eastern Mojave	0	1.89	4.1	4.25	2	Not reported
Goffs – 1984 (Turner et al. 1986)	Eastern Mojave	4%	1.57	4.29	4.27	0	Not reported
Goffs – 1985 (Turner et al. 1986)	Eastern Mojave	0	1.75	4.8	5.57	6	Not reported
Ward Valley – 1991 (Karl 1998)	Southeastern Mojave	13%	2	4.19	4.27	3	8.38±0.54
Ward Valley – 1992 (Karl 1998)	Southeastern Mojave	8%	1.84	3.19	3.52	1.5	6.68±0.57
Ward Valley – 1993 (Karl 1998)	Southeastern Mojave	10%	1.82	4.19	3.25	0	6.82±.042
Ward Valley – 1994 (Karl 1998)	Southeastern Mojave	28%	1.26	3.67	4.38	0	4.87±0.63
Ward Valley – 1995 (Karl 1998)	Southeastern Mojave	7%	1.68	4.08	3.77	3	6.76±0.47
Yucca Mountain – 1993-1995 (Mueller et al. 1998)	Northern Mojave	4%	1.5	5.1	4.8	0	7.9±0.8 (1993) 7.7±0.7 (1994) 6.7±0.7 (1995)
DTNA – 1992 (Wallis et al. 1999)	Western Mojave	0	1.67	4.4	4	0	7.1±2.7
DTNA – 1993	Western	28%	1.76	3.9	4	0	7.0±2.5

(Wallis et al. 1999)	Mojave						
Goffs – 1992 (Wallis et al. 1999)	Eastern Mojave	25%	1.7	4.2	4.1	0	7.1±2.8
Goffs – 1993 (Wallis et al. 1999)	Eastern Mojave	9%	1.67	4.2	4.7	0	7.3±3.1

Table 4. Reproductive rates for tortoises (female-only model, so clutch sizes were halved).

Age class	Number of Eggs per Season									Mean Eggs per Season	SD	Max
	0	1	2	3	4	5	6	7	8			
Young adult	0.33	0.12	0.21	0.22	0.21	0	0	0	0	2.5	2.5	4
Middle-aged adult	0.2	0.06	0.14	0.21	0.21	0.14	0.04	0	0	3.5	3.5	6
Old adult	0	0.05	0.09	0.12	0.16	0.19	0.17	0.13	0.09	4.83	5	8
Senescent adult	0	0.05	0.09	0.12	0.16	0.19	0.17	0.13	0.09	4.83	5	8

Table 5. Means of the maximum and median differences between the baseline model and threats scenarios.

	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
					Lower Bound	Upper Bound		
Maximum difference (Superior-Cronese)								
Human Presence	120	13455.6167	1522.37145	138.97286	13180.4365	13730.7968	10731.00	16314.00
Subsidized Predators	60	13228.1500	737.01197	95.14784	13037.7596	13418.5404	11586.00	15317.00
Disease	70	7505.5286	1269.11706	151.68850	7202.9183	7808.1389	4600.00	9718.00
Habitat Degradation on Land In-holdings	60	7143.7333	1361.03881	175.70935	6792.1397	7495.3269	4044.00	9897.00
Total	**310**	**10845.3677**	**3262.75545**	**185.31206**	**10481.7346**	**11211.0009**	**4404.00**	**16314.00**
Median difference (Superior-Cronese)								
Human Presence	120	10668.6167	1577.60473	144.01495	10383.4527	10953.7807	7627.00	13654.00
Subsidized Predators	60	9965.5333	650.85148	84.02456	9797.4006	10133.6661	8434.00	11279.00
Disease	70	5464.1714	1373.11702	164.11887	5136.7632	5791.5796	2458.00	7925.00
Habitat Degradation on Land In-holdings	60	4367.500	1286.12247	166.03770	4035.2593	4699.7407	1543.00	7291.00
Total	**310**	**8137.7677**	**3048.25461**	**173.12923**	**7797.1064**	**8478.4291**	**1543.00**	**13654.00**
Maximum difference (Gold Butte-Pakoon)								
Subsidized predators	60	5053.5000	532.54886	68.75176	4915.9280	5191.0720	3922.00	6093.00
Grazing	60	7453.7000	355.22093	45.85882	7361.9367	7545.4633	6844.00	8540.00
Human presence	90	6177.9556	711.08959	74.95542	6029.0207	6326.8904	4734.00	7641.00
Wildfire	210	3018.3286	535.43629	36.94861	2945.4888	3091.1683	1568.00	4403.00
Total	**420**	**4619.7548**	**1814.38149**	**88.53275**	**4445.7311**	**4793.7784**	**1568.00**	**8540.00**

Median difference (Gold Butte-Pakoon)							
Subsidized predators	60	3664.3667	473.62352	61.14453	3542.0167	3786.7166	2807.50	4844.50
Grazing	60	6353.1667	362.18920	46.75842	6259.6033	6446.7301	5715.00	7100.50
Human presence	90	4617.4944	680.33625	71.71374	4475.0008	4759.9881	3253.00	6105.00
Wildfire	210	1478.1857	472.86923	32.63108	1413.8575	1542.5139	409.00	2738.50
Total	**420**	**3159.6321**	**1905.34682**	**92.97140**	**2976.8837**	**3342.3806**	**409.00**	**7100.50**

Table 6. ANOVA of the means of the maximum and median differences

between the baseline model and threats scenarios.

	Sum of Squares	df	Mean Square	F	Sig.
Maximum difference (Superior-Cronese)					
Between Groups	2761209336.885	3	920403112.295	533.140	<0.001
Within Groups	528272759.193	306	1726381.566		
Total	**3289482096.077**	**309**			
Median difference (Superior-Cronese)					
Between Groups	2322330515.035	3	774110171.678	431.587	<0.001
Within Groups	548853040.243	306	1793637.386		
Total	**2871183555.277**	**309**			
	Sum of Squares	**df**	**Mean Square**	**F**	**Sig.**
Maximum difference (Gold Butte-Pakoon)					
Between Groups	1250240733.990	3	416746911.330	1342.898	<0.001
Within Groups	129098961.751	416	310334.043		
Total	**1379339695.740**	**419**			
Median difference (Gold Butte-Pakoon)					
Between Groups	1412212845.145	3	470737615.048	1798.188	<0.001
Within Groups	108902334.271	416	261784.457		
Total	**1521115179.416**	**419**			

Table 7. Bonferroni comparison each scenario against all other scenarios, correcting for multiple comparisons.

(I) scenario	(J) scenario	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
Maximum difference (Superior-Cronese)						
Human presence	Subsidized predators	227.46667	207.74874	1.000	-324.2144	779.1477
	Disease	5950.08810	197.60847	<.001	5425.3347	6474.8415
	Habitat Degradation on Land In-holdings	6311.88333	207.74874	<.001	5760.2023	6863.5644
Subsidized predators	Human presence	-227.46667	207.74874	1.000	-779.1477	324.2144
	Disease	5722.62143	231.16146	<.001	5447.3903	6336.4754
	Habitat Degradation on Land In-holdings	6084.41667	239.88758	<.001	5108.7674	6721.4431
Disease	Human presence	-5950.08810	197.60847	<.001	-6474.8415	-5425.3347
	Subsidized predators	-5722.62143	231.16146	<.001	-6336.4754	-5108.7674
	Habitat Degradation on Land In-holdings	361.79524	231.16146	0.712	-252.0588	975.6492
Habitat Degradation on Land In-holdings	Human presence	-6311.88333	207.74874	<.001	-6863.5644	-5760.2023
	Subsidized predators	-6084.41667	239.88758	<.001	-6721.4431	-5447.3903
	Disease	-361.79524	231.16146	0.712	-975.6492	252.0588
Median difference (Superior-Cronese)						
Human presence	Subsidized predators	703.08333	211.75678	0.006	140.7588	1265.4078

	Disease	5204.44524	201.42088	<.001	4669.5680	5739.3225
	Habitat Degradation on Land In-holdings	6301.11667	211.75678	<.001	5738.7922	6863.4412
Subsidized predators	Human presence	-703.08333	211.75678	0.006	-1265.4078	-140.7588
	Disease	4501.36190	235.62120	<.001	3875.6650	6247.3497
	Habitat Degradation on Land In-holdings	5598.03333	244.51567	<.001	4948.7169	5127.0588
Disease	Human presence	-5204.44524	201.42088	<.001	-5739.3225	-4669.5680
	Subsidized predators	-4501.36190	235.62120	<.001	-5127.0588	-3875.6650
	Habitat Degradation on Land In-holdings	1096.67143	235.62120	<.001	470.9745	1722.3684
Habitat Degradation on Land In-holdings	Human presence	-6301.116667	211.75678	<.001	-6863.4412	-5738.7922
	Subsidized predators	-5598.03333	244.51567	<.001	-6247.3497	-4948.7169
	Disease	-1096.67143	235.62120	<.001	-1722.3684	-470.9745
Maximum difference (Gold Butte-Pakoon)						
Subsidized predators	Grazing	-2400.20000	101.70776	<.0001	-2669.8207	-2130.5793
	Human presence	-1124.45556	92.84606	<.0001	-1370.5844	-878.3267
	Wildfire	2035.17143	81.54763	<.0001	1818.9940	2251.3489
Grazing	Subsidized predators	2400.20000	101.70776	<.0001	2130.5793	2669.8207
	Human presence	1275.74444	92.84606	<.0001	1029.6156	1521.8733
	Wildfire	4435.37143	81.54763	<.0001	4219.1940	4651.5489
Human presence	Subsidized predators	1124.45556	92.84606	<.0001	878.3267	1370.5844
	Grazing	-1275.74444	92.84606	<.0001	-1521.8733	-1029.6156
	Wildfire	3159.62698	70.18502	<.0001	2973.5710	3345.6829
Wildfire	Subsidized	-2035.17143	81.54763	<.0001	-2251.3489	-1818.9940

	predators					
	Grazing	-4435.37143	81.54763	<.0001	-4651.5489	-4219.1940
	Human presence	-3159.62698	70.18502	<.0001	-3345.6829	-2973.5710
Median difference (Gold Butte-Pakoon)						
Subsidized predators	Grazing	-2688.80000	93.41386	<.0001	-2936.4341	-2441.1659
	Human presence	-953.12778	85.27479	<.0001	-1179.1857	-727.0698
	Wildfire	2186.18095	74.89771	<.0001	1987.6320	2384.7299
Grazing	Subsidized predators	2688.80000	93.41386	<.0001	2441.1659	2936.4341
	Human presence	1735.67222	85.27479	<.0001	1509.6143	1961.7302
	Wildfire	4874.98095	74.89771	<.0001	4676.4320	5073.5299
Human presence	Subsidized predators	953.12778	85.27479	<.0001	727.0698	1179.1857
	Grazing	-1735.67222	85.27479	<.0001	-1961.7302	-1509.6143
	Wildfire	3139.30873	64.46169	<.0001	2968.4250	3310.1925
Wildfire	Subsidized predators	-2186.18095	74.89771	<.0001	-2384.7299	-1987.6320
	Grazing	-4874.98095	74.89771	<.0001	-5073.5299	-4676.4320
	Human presence	-3139.30873	64.46169	<.0001	-3310.1925	-2968.4250